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Holocene History of Alpine Vegetation and Forestline on Pyhäkero Mountain, Northern Finland

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Abstract

Paleoecological analyses were carried out from two sediment cores from lake sites at the alpine treeline on Pyhäkero mountain, the northernmost peak of an isolated mountain range, Pallastunturi-Ounastunturi, south of the polar forestline in western Finnish Lapland. Plant macrofossils, supported by pollen data, show presence of pine (*Pinus sylvestris*) and birch (*Betula pubescens*) on the top of the mountain from 9500 cal yr BP (birch) and 8300 cal yr BP (pine) up to 2000 cal yr BP (pine) and 1500 cal yr BP (birch). However, the major floristic elements of the modern alpine vegetation, as evidenced by plant macrofossils of a number of typical alpine taxa, including *Salix cf. polaris*, show persistence through the warmer periods of the Holocene, and indicate that the scattered pine-birch forest never completely replaced the low-alpine plant communities. The current low-alpine vegetation on the mountain top has therefore long continuity from the time of regional deglaciation. Dispersal of these alpine species took place primarily during the deglaciation phase and it is unnecessary to invoke dispersal of the arctic-alpine plants from the arctic regions of Fennoscandia during the mid- or late-Holocene to explain the origin of the alpine flora of the mountain range.

Introduction

Although the postglacial history of the polar forestline of northern Fennoscandia has been intensively studied (e.g., Aario, 1943; Hyvärinen, 1975, 1976; Eronen, 1979; Eronen and Hyvärinen, 1982; Seppä, 1996; Jensen et al., 2002; Seppä et al., 2002), the alpine forestlines of isolated mountain ranges south of the polar forestline have not been given the same attention. In eastern Fennoscandia, there is a major vegetational difference between the polar (latitudinal) forestline and the alpine (altitudinal) forestlines. At the polar forestline, pine (*Pinus sylvestris*) reaches farther north than spruce (*Picea abies*) and the vegetation north of the limit of the continuous pine-formed conifer forest is characterized by a wide zone of mountain birch (*Betula pubescens* ssp. *tortuosa*) forest. This forestline pattern is not repeated along the altitudinal transects of the mountains of central Lapland (northern Fennoscandia), located farther south of the polar forestline. The highest altitudinal limit of the continuous boreal forest there is usually formed by a mixture of the three species, with individual pines and spruces often growing at higher altitudes than birch (Heikinheimo, 1920, 1921; Hustich, 1937; Veijola, 1997). The reason for this difference between the polar and alpine forestlines is not precisely known, but Hämet-Ahti (1963) and Kullman (1981), for example, have debated the influence of the more oceanic climate (colder summers, milder winters, deep, durable snow) of subarctic Fennoscandia, closer to the Arctic sea coast, which favors mountain birch. The more continental climate of the mountains, particularly higher summer temperatures and earlier snowmelt, may support higher altitudinal distributions of pine and spruce.

Ecophysiological studies of the principal tree species of the polar and alpine forestlines in northern Fennoscandia have established the sensitivity of their regeneration and growth to the climatic conditions. In these cold-stressed environments, the flower bud initiation and subsequent anatomical maturation of the seeds of pine and spruce are dependent on the summer temperatures (Heikinheimo, 1921; Eide, 1932; Sarvas, 1962; Chung, 1981; Henttonen et al., 1986; Luomajoki, 1993a,

1993b), and the regeneration of pine is limited to a few adequately warm periods or “key years” per century (Sirén, 1961; Sarvas, 1962; Hustich, 1978; Henttonen et al., 1986). Similarly, the juvenile and radial growth of the trees, as well as the growth in length of annual shoots of secondary branches, show correlation with the high-frequency variations of summer temperatures (Hustich, 1948, 1949, 1978; Sirén, 1961; Kullman, 1986, 1996; Lindholm, 1996; Kirchner, 2001). The cumulative effect of a short sequence of “key years” can lead to a rapid upwards and northwards shift of the pine forestline. This was observed in Lapland after a period of warm summers in the 1930s when new pine seedlings became established around the isolated pines in the mountain birch zone and in the alpine zone of the mountains (Hustich, 1959, 1978). The rapid advance of pine forestline was subsequently retarded by the cold summers in the 1960s (Mikola, 1971; Kallio, 1975; Hustich, 1978).

One reason for the small number of studies into the Holocene history of the alpine forestlines of the mountains in eastern Fennoscandia is the scarcity of suitable lake sites above the forestline for paleoecological research and vegetation reconstructions. In the highest and largest of the isolated mountains in western Finnish Lapland, close to the northernmost peak of the Pallastunturi-Ounastunturi mountain range, lies Pyhäkero mountain, one of the few sites with several lakes located at different altitudes. The modern alpine vegetation and forestline patterns of this mountain range were studied by Sandman (1893) and Hustich (1937, 1940, 1959). Hustich (1959) observed the establishment of new pine seedlings on the top of the mountain, at altitude of over 600 m a.s.l., and the subsequent distinct rise of the distribution limit of pine in response to the warm summers in the 1920s and 1930s. The question of whether these pines represented the highest altitude ever during the postglacial period was debated, but, due to the lack of paleoecological data, remained unanswered.

In this paper we present plant macrofossil and pollen evidence from two lake sites on Pyhäkero mountain, lying above the limit of continuous forest at ca. 500 m a.s.l., which is formed by birch and pine. The main aim of the paleoecological reconstructions from these lake

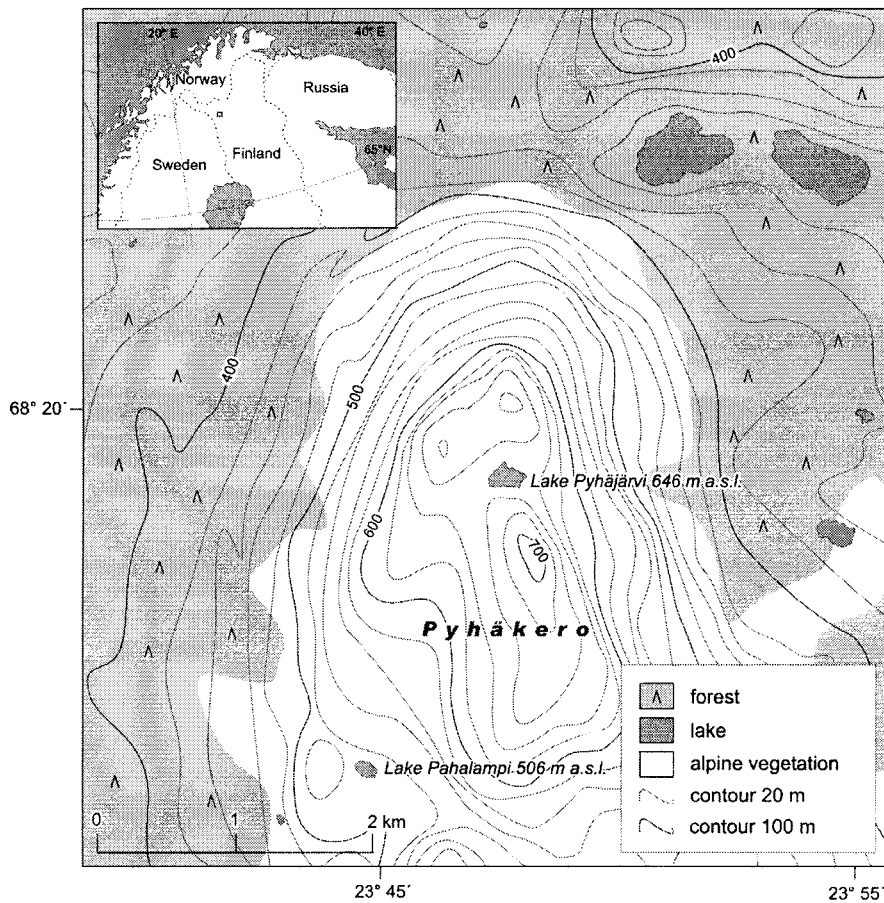


FIGURE 1. Location of the study area. The altitudinal limit of the continuous forest (forestline) is at 450–500 m a.s.l. but there are scattered pines and birches above this altitude.

sites was to use the combination of pollen and plant macrofossils to study the history of the modern alpine vegetation of the mountain top and to determine the long-term dynamics of the alpine forestline during the Holocene. This approach can provide a paleoecological perspective on current discussion about the recent altitudinal distribution changes of alpine plants and about the vulnerability of the alpine vegetation to predicted future warming (Grabherr et al., 1994; Körner, 1999; Odland and Birks, 1999; Klanderud and Birks, 2003). The emphasis in this study was placed on plant macrofossil analysis because of their potential for a higher taxonomic and spatial resolution than pollen alone (Birks, 1973, 2001, 2003; Hannon, 1999). Pollen can disperse over considerable distances, particularly in open forest and nonforest vegetation. Macrofossil records tend, however, to be less continuous and do not deliver such a well-developed basis for statistical analyses.

Study Area

Pyhäkero mountain (711 m a.s.l.) in northern Finland (Fig. 1), is the northernmost peak of Pallastunturi-Ounastunturi mountain range, a chain of residual mountains rising 400 to 500 m above the surrounding peneplain. Bedrock consists of gray quartzite (Johansson, 1998). During the last two million years, the Pallastunturi-Ounastunturi mountain range has been frequently covered by ice sheets, which has given rise to the typically glacially-shaped mountains and gentle relief of the mountain range. The last deglaciation took place at ca. 10,500–10,000 cal yr BP (Lundqvist, 1991). Thin till deposits cover most of the mountain top (Johansson, 1998).

The climate is northern boreal on the surrounding peneplain but becomes progressively colder and windier towards the top of the mountain. The closest meteorological station with a record from the

Climate Normals period 1961–1990 is in Muonio, ca. 37 km south of Pyhäkero mountain. The annual mean temperature there is -1.7°C , July mean temperature 13.0°C , and January mean temperature -16.2°C . The annual precipitation is 450 mm (Finnish Meteorological Institute, 1991).

Pyhäkero mountain is located within the northern boreal conifer forest zone (Sjörs, 1967; Ahti et al., 1968) but the vegetation of the mountain top, above the alpine forestline, is treeless, low-alpine heath. The mountain top therefore forms a biogeographically azonal, isolated island of alpine vegetation within the boreal zone (Figs. 1, 2). The forest line is located at about 500 m a.s.l. but there are scattered pines and birches above this altitude. The alpine plant communities of the mountain top are characterized by dry, oligotrophic heath vegetation, with *Empetrum nigrum* and *Betula nana* as the dominant vascular plants, and a lichen-rich ground layer. Other typical vascular plant species of the alpine heaths are *Juniperus communis*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Loiseleuria procumbens*, *Phyllodoce caerulea*, *Arctostaphylos alpina*, and *Diapensia lapponica*. Moister sites, such as the shallow bedrock depressions and the lake and stream shores, support richer vegetation, with *Salix* spp. (e.g., *S. herbacea*, *S. glauca*), *Oxyria digyna*, sedges, grasses, and mosses. On the slopes between the mountain top and the forestline, *Vaccinium myrtillus*-dominated heaths are common.

The two lakes studied are located on the top (Lake Pyhäjärvi) and on the slope (Lake Pahalampi) of Pyhäkero mountain (Fig. 1). Lake Pyhäjärvi is the higher lake (Fig. 2), located in a shallow, gently-sloped depression at 646 m a.s.l., 400 m north of the highest peak of the mountain. Its maximum depth is 400 cm and size ca. 5 ha. The lake has a small, seasonally-dry outlet in the southwest. The second lake, Lake Pahalampi, is located in a shallow depression on the western slope of the mountain, at 506 m a.s.l. The continuous birch-pine forest begins, first sparsely and then more densely, right below the lake ca. 500 m a.s.l. Some scattered birches grow close to the shore of the lake.

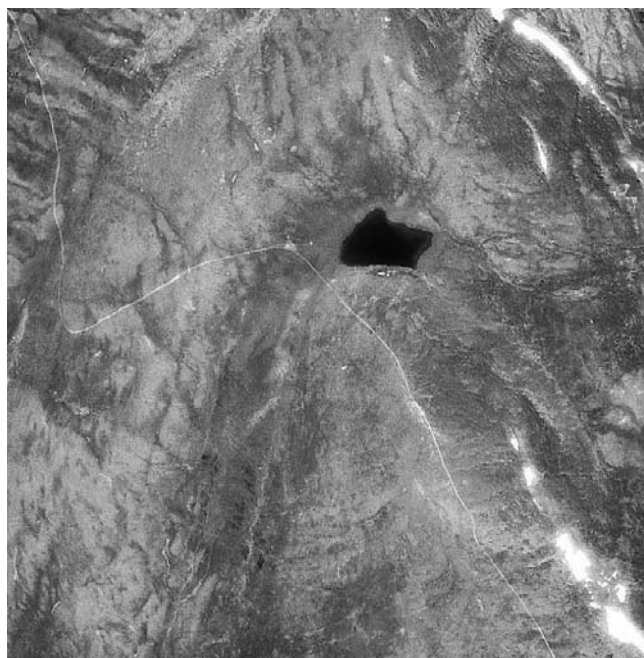


FIGURE 2. An aerial photograph of the Pyhäkero mountain top, with scale 1:20,000. Lake Pyhäjärvi is in the center of the photograph. The low-alpine zone of the mountain top is characterized by dry, oligotrophic heath vegetation, with *Empetrum nigrum* and *Betula nana* as the dominant vascular plants, and a lichen-rich ground layer. Moister sites around the lake support richer vegetation, with *Salix* spp. (e.g., *S. herbacea*, *S. glauca*), *Oxyria digyna*, sedges, grasses, and mosses.

Methods

At each lake, a series of sediment cores was collected from the surface of the ice in April 2000 with a rod-operated Livingstone corer. A 219-cm-long core was sampled from the center of Lake Pyhäjärvi and a 370-cm-long core from Lake Pahalampi.

PLANT MACROFOSSIL ANALYSIS

Plant macrofossil analysis was carried out on 5-cm subsamples, soaked overnight in 5% NaOH and washed through a sieve, mesh size 285 μm . All fossil remains were initially identified using an identification key (Bertsch, 1941) and subsequently matched with specimens from a reference collection. Macroscopic charcoal (>285 μm) was systematically counted at both sites. The results for plant macrofossils are presented as concentration per unit volume and the diagrams were drawn up using the programs TILIA and TILIA.GRAPH (Grimm, 1990).

POLLEN ANALYSIS

Pollen analysis was carried out only from Lake Pyhäjärvi sediment core. The pollen samples were prepared with standard KOH, HF, and acetolysis methods (Moore et al., 1991) and analyzed to the lowest possible taxonomic level, mainly with the help of the pollen guide of Moore et al. (1991) and pollen reference samples. Each 1-cm³ subsample was spiked with two *Lycopodium* tablets (Stockmarr, 1972) for the pollen concentration and pollen accumulation rate calculations. A minimum of 500 pollen and spores of terrestrial plants was determined from each level, except from the lowermost sample where the pollen concentration was low. A total of 52 pollen samples were analyzed from the core.

TABLE 1

Radiocarbon dates of the two sediment cores

	Depth (cm)	¹⁴ C age (yr)	Cal yr BP age (2 s.d. age range)
Lake Pyhäjärvi			
AAR-6637	256–260	4100 ± 50	4570 (4820–4440)
AAR-6638	272–276	2550 ± 45	2720 (2760–2470)
AAR-6639	280–284	2430 ± 45	2410 (2710–2350)
AAR-6640	316–320	3850 ± 45	4250 (4410–4110)
AAR-6641	332–336	4010 ± 60	4470 (4620–4330)
AAR-6642	412–416	7680 ± 70	8430 (8600–8360)
AAR-6643	428–432	8510 ± 75	9500 (9590–9430)
Lake Pahalampi			
AAR-7587	316–320	680 ± 40	660 (700–560)
AAR-7588	336–340	1690 ± 40	1570 (1700–1500)
AAR-7589	368–372	2490 ± 40	2590 (2740–2390)
AAR-7590	452–456	4230 ± 50	4830 (4870–4620)
AAR-7591	555–560	6790 ± 60	7640 (7710–7550)
AAR-7592	595–600	8915 ± 60	10140 (10200–9770)

The percentages of terrestrial pollen and spore taxa were calculated on the basis of their total sum. Percentages of aquatics were calculated on the basis of the total sum of terrestrial taxa plus aquatic taxa, and the percentages of *Sphagnum* on the basis of the total sum of terrestrial taxa plus *Sphagnum*. The pollen diagrams were drawn with the programs TILIA and TILIA.GRAPH (Grimm, 1990).

DATING

Selected plant macrofossils, where available, were sent to radiocarbon laboratories in Denmark (Aarhus) and Sweden (Uppsala) to establish time scales from each site. Otherwise raw sediment was used for dating purposes (Table 1). The radiocarbon dates were calibrated using CALIB 4.2 program (Stuiver and Reimer, 1993) and the INTCAL98 calibration data (Stuiver et al., 1998), using bidecadal tree-ring data set A and method A, and applying 10 sample smoothing. The chronology of Lake Pyhäjärvi core is based on seven calibrated radiocarbon dates and an assumed modern age for the core top and the chronology of the Lake Pahalampi core on six calibrated radiocarbon dates and an assumed modern age for the core top.

Results

CHRONOLOGY

Before the age-depth modelling, the reliability of the calibrated radiocarbon dates was assessed. At Lake Pyhäjärvi, dates from 256 to 260 cm and 272 to 276 cm are older than the date from 280 to 284 cm. These two dates are therefore likely too old, possibly due to the re-deposition of the dated moss samples from the lake catchment. The presumed redeposition is supported by the even sedimentation rate when these two dates are excluded from the age-depth model (Fig. 3). Chronologies for the two sites were derived by fitting a second-order polynomial age-depth curve (Lake Pyhäjärvi) and a third-order polynomial age-depth curve (Lake Pahalampi) to the calibrated radiocarbon dates.

FORESTLINE AND VEGETATION HISTORY

The extrapolated basal ages of the two sediment cores, ca. 10,400–10,300 cal yr BP, are consistent with the estimated regional deglaciation (Lundqvist, 1991). The pollen data suggests that the first postglacial vegetation of the mountain consisted of rich herb communities and this

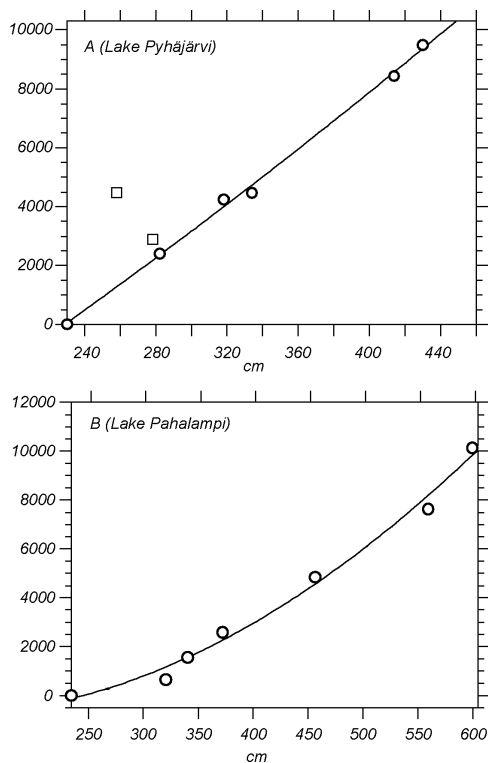


FIGURE 3. Age-depth models of Lake Pyhäjärvi (a) and Lake Pahalampi (b) cores. The model for Lake Pyhäjärvi core is based on a second-order polynomial function and for Lake Pahalampi core on a third-order polynomial function. The two radiocarbon dates which were excluded from the Lake Pyhäjärvi age-depth curve are indicated by the squares.

is confirmed by the plant macrofossil results (Figs. 4, 5). The most striking feature of the earliest plant macrofossil and pollen assemblages is the floristic difference between the two sites. Lake Pyhäjärvi has high values of *Sagina* seeds and the corresponding pollen type, Caryophyllaceae undiff., as well as *Rumex acetosella* nuts and *Rumex acetosella*-type pollen (Figs. 4, 5). The Lake Pahalampi record, by contrast, shows presence of macrofossils of *Sedum*, Brassicaceae, and *Empetrum* (Fig. 6). These features indicate major vegetational difference between the mountain top and the lower slopes and reflect plant communities which do not have analogs in the modern alpine vegetation of Pallastunturi–Ounastunturi mountain range or elsewhere in northern Fennoscandia today (Hustich, 1937, 1940; Haapasaaari, 1988; Oksanen and Virtanen, 1995). This may be a consequence of the plant dispersal history and the unique edaphic and climatic conditions in the recently deglaciated terrain. However, the early postglacial appearances of plant macrofossils and/or pollen types of Poaceae, *Carex*-type, *Salix* undiff., *Betula nana*, Ranunculaceae, *Vaccinium* sp., and *Empetrum* suggest that the most common floristic elements of the modern alpine heaths were also present soon after the deglaciation.

The rise of *Betula* pollen accumulation rate (PAR) at 10,000 cal yr BP in the Lake Pyhäjärvi pollen record and the appearance of *B. pubescens* macrofossils in Lake Pahalampi record at 9500 cal yr BP indicate that the first postglacial forest and alpine forestline on Pyhäkero mountain was formed by birch (Figs. 4, 6). This is in agreement with reconstructed forest pattern in the arctic and alpine regions of northern Fennoscandia where abundant *Betula pubescens* macrosubfossil records show the establishment of birch forest during the early Holocene before the immigration of pine (Barnekow, 1999, 2000; Jensen et al., 2002). As in the early Holocene records from arctic

Fennoscandia, the field layer of the birch forest on Pyhäkero mountain was characterized by grasses, ferns, and lycopods, corresponding with the field layer of the modern oceanic mountain birch forests of the arctic forestline (Hämet-Ahti, 1963).

The rise of *Pinus* pollen values reflects the gradual immigration and expansion of pine at 9000–8000 cal yr BP in the area and its local presence is shown by the occurrence of *Pinus* needles in Lake Pahalampi core at ca. 8300 cal yr BP (Figs 4, 6). The immigration history of pine on Pyhäkero mountain agrees with the results from the arctic forestline: according to the macrofossil, stomatal, and pollen evidence from a number of sites from the Kola Peninsula to northwestern Norway and northern Sweden (Abisko), the initial immigration of pine took place at ca. 9500–9000 cal yr BP and subsequent development of denser pine forest at ca. 8500–8000 cal yr BP (Hyvärinen, 1975; Seppä, 1996; Barnekow, 1999, 2000; Snyder et al., 2000; Gervais et al., 2002; Jensen et al., 2002; Seppä et al., 2002). On Pyhäkero mountain, this change is accompanied by typical pollen-stratigraphical features with a decrease in grasses, ferns, and lycopods and replacement by ericaceous dwarf shrubs. This change suggests that the pine forest understory has been dominated by similar plant communities since the expansion of pine in Finnish Lapland. Analogs can be observed in the modern northernmost pine forests in Finnish Lapland.

The occurrence of pine macrofossil cone scales in the Lake Pyhäjärvi record suggests local presence of pine close to the top of the Pyhäkero mountain during the Holocene. The establishment of scattered pine stands may have happened already by 8000–7500 cal yr BP, as at that time *Pinus* PAR values exceed their modern level. However, the low number of pine macrofossils, lower *Pinus* pollen percentage values than in the modern samples from dense pine forest (Hicks, 2001), and continuous occurrence of plant macrofossils of the typical alpine plant taxa, notably *Salix* cf. *polaris* leaves (Fig. 4), refute the theory of dense pine or pine-birch forest covering the mountain top during the postglacial period. The more likely scenario is that alpine *Betula nana*–*Empetrum* plant communities and snowbed plant communities co-existed with the discontinuous pine-birch forest. Pine probably occurred as individual trees or scattered stands, located mostly on higher sites where snow did not gather and which were snow free early in the spring. This pattern is currently observed for pine at its extreme distribution limit in northern Fennoscandia. The alpine plant communities typical of snow-rich sites were likely confined to depressions, such as the shores of the Lake Pyhäjärvi basin where they dominate at present.

The rise of *Picea* pollen curve suggests that spruce became regionally established at ca. 5500 cal yr BP. The modern northern limit of continuous spruce forest is located 15 to 20 km south of Pyhäkero mountain. The absence of macrofossil evidence for spruce and low *Picea* pollen values at Lake Pahalampi suggest that the distribution limit of spruce never reached Pyhäkero mountain. The lack of evidence of fluctuations of the northern limit of spruce is in line with the interpretations of the data from the polar forestline (Hyvärinen, 1975; Seppä et al., 2002). However, on Pyhäkero mountain this does not necessarily reflect climatic stability since the altitudinal limit of spruce may have been partly, or fully, constrained by nonclimatic, edaphic factors, as spruce does not find good seed beds and generally does not grow well on dry, exposed mountain slopes (Hustich, 1959).

The gradual decline of the *Pinus* PAR values starts at 3500 cal yr BP (Fig. 4). This may reflect a gradual reduction in the number of pines growing on the mountain slopes. The recovery of *Pinus* cone scales in the fossil record, however, shows that some individual pines persisted closer to the mountain top up until 2000 cal yr BP. Between this time period and the observations of Hustich (1959) that scattered pines had recently become established on the mountain top, we have no evidence for occurrence of pine on the mountain top. Nevertheless, the possibility exists of episodic pine forestline shifts and transient

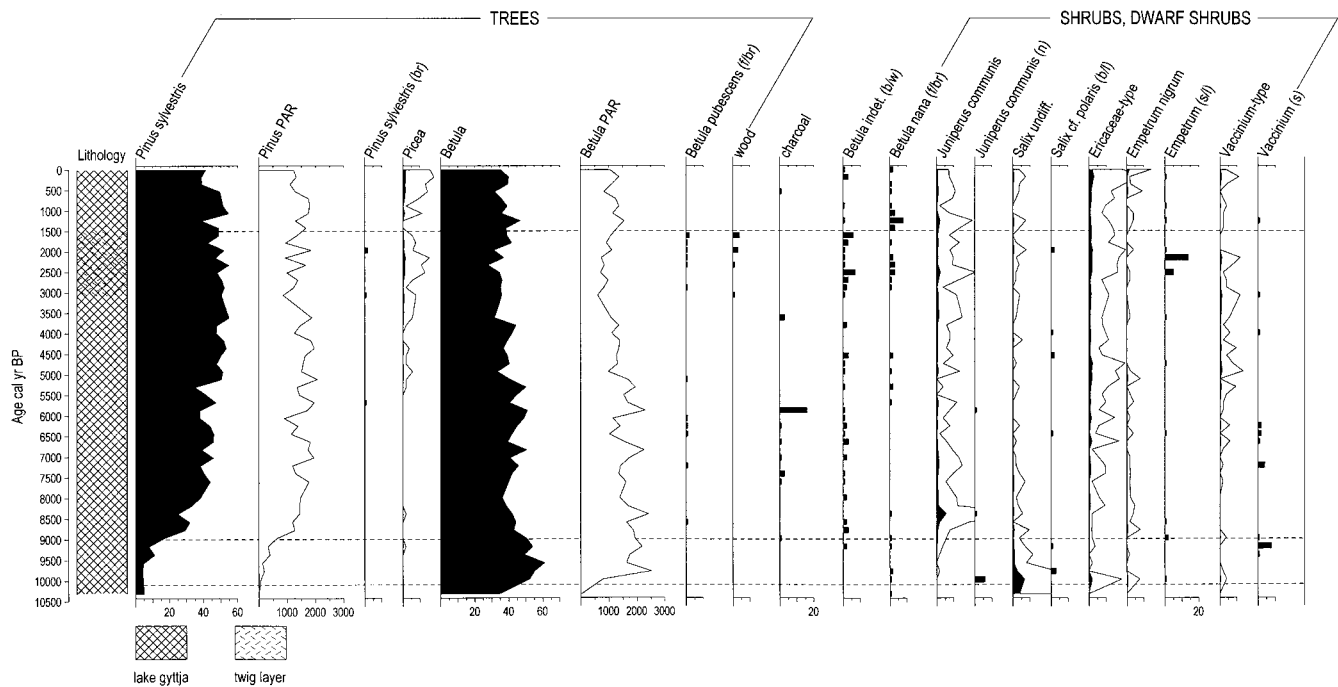


FIGURE 4. An abbreviated plant macrofossil (bars) and pollen (silhouettes) diagram of the trees, shrubs, and dwarf shrubs of the Lake Pyhäjärvi core. Plant macrofossils are indicated as numbers of fossil per unit volume. The pollen percentage values (% of total terrestrial pollen and spores) are shown with a 10× exaggeration. Pollen accumulation rate values (PAR, grains cm⁻².yr⁻¹) of *Pinus* and *Betula* are shown. Abbreviations of the plant macrosubfossil types: b = bud bracts, br = bracts, f = fruits, l = leaves, n = needles, nt = nuts, s = seeds, w = wood.

occurrences of pine stands during for example the Medieval Warm Period (about 700 to 1000 cal yr BP), when the advance of the altitudinal pine forestline is documented by pine megafossil records from the Khibiny mountains on the Kola Peninsula (Hiller et al., 2000) and from the coastal northern Norway (Kirchhefer, 2001).

Betula pubescens fruits and bracts and indeterminate wood remains disappear from the Lake Pyhäjärvi core at ca. 1500 cal yr BP.

At that level there is a layer of twigs and bark of deciduous trees and shrubs in the sediment core, suggesting sudden break-up of the sparse birch forest on the mountain top (Fig. 4). There are no indications of any major cooling or forestline decline at that time in the previous paleoclimatological and paleoecological records in northern Fennoscandia, many of which have higher temporal resolution than the current data (e.g., Eronen and Zetterberg, 1996; Seppä and Birks, 2001,

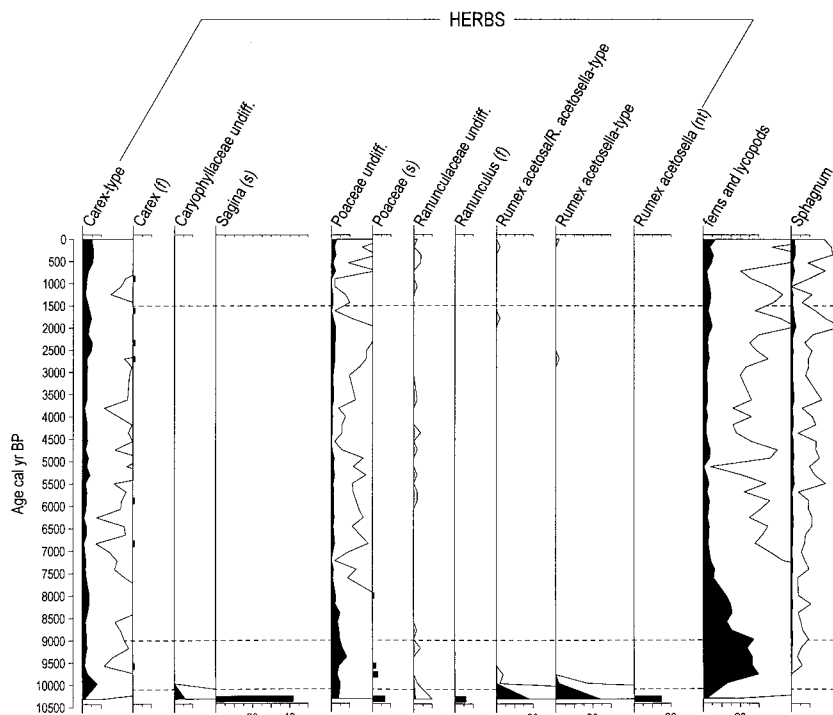


FIGURE 5. An abbreviated plant macrofossil and pollen diagram of the herbs, peridophytes and *Sphagnum* of the Lake Pyhäjärvi core. Explanations as in Figure 4.

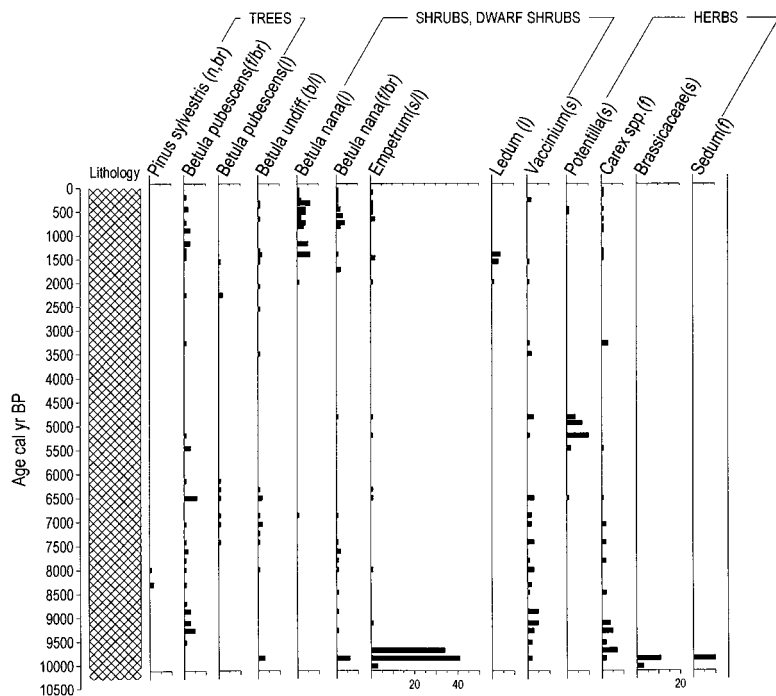


FIGURE 6. A plant macrofossil diagram for the Lake Pahalampi core, showing only the most common taxa. Explanations as in Figure 4.

2002; Seppä et al., 2002). The death of the birches may therefore have been a rapid, local event, possibly caused by a local disturbance such as a storm or outbreak of *Epirrita autumnata* insect pathogen. Such an outbreak of *Epirrita* destroyed about 5000 km² of mountain birch forest in northern Finland in 1965 (Kallio and Lehtonen, 1973, 1975). Although mountain birch is capable of recovery from mechanical damage by growth from basal sprouts, the subsequent recovery of the forest has largely failed at the high-altitude regions (Kallio and Lehtonen, 1975; Seppälä and Rastas, 1980; Lehtonen, 1987). This may be due to the windier and colder local climatic conditions, which often follow the change from sparse forestline forest to open tundra (e.g., Grace, 1989; Arsenault and Payette, 2000).

During the last 1500 yr the macrofossil and pollen assemblages of Lake Pyhäjärvi were dominated by *Vaccinium*, *Empetrum*, and *Ericaceae*-type. The fossil record corresponds well with the floristic composition of the modern low-alpine *Betula nana*–*Empetrum* and *Empetrum*–*Vaccinium myrtillus* plant communities, that largely cover the mountain top of Pyhäkero mountain, as well as other mountains of northern Fennoscandia, with the exception of snow-bed sites and moister hollows (Kalliola, 1939; Hedberg et al., 1952; Hämet-Ahti, 1963; Jonasson, 1981; Haapasaaari, 1988; Oksanen and Virtanen, 1995).

Discussion and Conclusions

New evidence of the timing and pattern of the postglacial immigration of pine to Pyhäkero mountain agrees with earlier vegetation reconstructions from the arctic regions of Fennoscandia. In addition, the current evidence suggests that the range limit of pine on the Pallastunturi-Ounastunturi mountain range reached at least an altitude of ca. 650 m a.s.l. and corresponds with the recent estimations of the maximum altitudinal limits of the pine forestline during the Holocene in northern Fennoscandia. In Abisko, northern Sweden, plant macrofossils recorded from lake sites show that at 5500–4500 cal yr BP the alpine distribution limit of pine was above the altitude of 625 m a.s.l., but below 1000 m a.s.l. (Barnekow, 1999, 2000). Stomatal and pollen evidence suggest that in northwestern Finnish Lapland, pine reached an altitude of ca. 700 m a.s.l. at 8000–4000 cal yr BP (Seppä et al.,

2002). In conjunction with the current evidence, these data sets suggest that maximal altitudinal limit of pine in northern Swedish Lapland and northwestern Finnish Lapland during the Holocene was above 700 m a.s.l.

Our interpretation of the forestline and alpine vegetation history of Pyhäkero mountain is of relevance for the classical debate about the ancestry of the modern alpine plant communities and dispersal history of the alpine flora of the isolated mountains located within the boreal forest. Based on the theories of Sernander (1894), the question was raised about the origin and spread of the modern alpine flora in the Pallastunturi-Ounastunturi mountain range (Hustich, 1937). If dense pine-birch forest had covered the current alpine vegetation belt at ca. 500–700 m a.s.l. during the Holocene thermal maximum, the alpine plant communities would have been replaced and such alpine taxa as *Salix herbacea*, *S. polaris*, *Oxyria digyna*, and *Arctostaphylos alpina*, for example, could have become extinct locally. As this mountain is surrounded by boreal forest, the re-establishment of the alpine plants after the retreat of the forestline would have required propagule dispersal from the arctic vegetation zone of northern Fennoscandia, through the boreal forest. This hypothesis is consistent with the recent ecological theories stressing the climatic sensitivity of the alpine plant communities consisting of competition-intolerant species with narrow habitat demands, and with the predicted disappearance of many alpine species on such mountains where no refugial habitats exist (e.g., Grabherr et al., 1994, 1995; Sætersdal and Birks, 1997; Gottfried et al., 1999; Körner, 1999; Klanderud and Birks, 2003). In northern Swedish mountains, a substantial reduction of true alpine grounds or even replacement by forest during the early Holocene has been suggested (Kullman, 1999), but this hypothesis is refuted by plant macrofossil evidence from high-altitude sites by Barnekow (1999, 2000).

Our evidence indicates that the major floristic elements of the modern alpine vegetation have persisted on Pyhäkero mountain throughout much of the Holocene, apart from the earliest postglacial period. Despite the higher Holocene forestlines and occurrences of pine and birch on the top of the mountain it is likely that, during the whole of the Holocene, Pyhäkero mountain top included an adequately rich mosaic of open microsites so that most of the modern alpine plant

species survived through the warmer periods of the Holocene. Their dispersal to Pyhäkero mountain has, therefore, predominantly happened during the deglaciation phase, and there is no need to invoke complex Holocene dispersal patterns from the far north of Fennoscandia during the late Holocene. In this sense, the current low-alpine flora of Pyhäkero represents a Holocene continuum or “relict vegetation” as discussed by Semander (1897) and Hustich (1937).

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